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Control of Species Density in Herbaceous Vegetation

J. P. Grime

Nature Conservancy Grassland Research Unit,
Department of Botany,
The University, Sheffield, England

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Data from vegetation surveys and experiments have been used to investigate the impact of environmental stress and of certain forms of management (grazing, mowing, burning and trampling) upon the density of species of flowering plants in herbaceous vegetation. Simple models are proposed to describe the effects of environmental stress and management upon species density and to account for the role of interspecific competition in these effects. It is suggested that the maximum potential relative growth-rates of the constituent perennial species may be used to provide an index of the stability of vegetation of high species density.

1. Introduction

A major problem in conserving wild-life in Britain arises from difficulties in maintaining or reconstructing the so-called "species-rich" plant communities here arbitrarily defined as herbaceous vegetation in which the mean density of flowering plants, recorded in square quadrats of one square metre, exceeds 20 species/m^2. A high proportion of the records of rare or declining species in Britain refer to animals and plants associated with species-rich vegetation (Pigott and Walters, 1954; Clapham, Tutin and Warburg, 1962; Perring and Walters, 1962; Perring, 1968; Heath, 1970). A related problem in the fields of landscape design and reclamation is the low species density

and associated visual monotony of many derelict or newly-created habitats, e.g. spoil heaps and motorway banks.

Attempts to understand the control of species density are complicated by the fact that the primary controlling factors appear to vary with ecological situation. As a guide to appropriate management, there is a need for simple objective criteria with which to recognize the particular regulation mechanism operative at individual sites.

An attempt has been made to describe the major factors affecting species density in the herbaceous vegetation in an area of Northern England, and to devise criteria which allow their influence to be distinguished.

The data used in this paper are derived from three sources.

(i) *Measurements of species density.* During the period 1965–71 two vegetation surveys (Lloyd, Grime and Rorison, 1971; Grime and Hodgson, unpublished) have been carried out. These provide measurements of species density in approximately 3000 one square metre samples from a wide range of herbaceous vegetation types in an area of 900 square miles around Sheffield, Yorkshire. The one square metre quadrat was chosen because it is small in relation to many of the patterns of variation in species density imposed by topography, substratum and management, and by the morphology of the larger herbaceous species. The quadrat data include site information and records of the frequency of each species. It is therefore possible to relate variation in species density to features of environment, to management and to field or laboratory characteristics of the component species.

(ii) *Growth-analysis in a controlled environment.* By means of a screening procedure (Hunt, 1970), 135 flowering plants, including many of the commoner herbaceous species encountered in the surveys, have been subjected to a standardized analysis of dry matter production over the period 2–5 weeks after germination, in a productive growth-room environment [daylength 18 hours; temperature 20°C (day) 15°C (night); $38 \cdot 0$ W m^{-2} visible radiation flux density; relative humidity $> 70\%$; medium: sand+Hewitt's solution]. Whilst it is clear that the environment selected does not approach the conditions optimal for the growth of certain of the species examined, published data (Bradshaw *et al.*, 1964; Jarvis and Jarvis, 1964; Grime and Jeffrey, 1965; Grime, 1965; Clarkson, 1967; Myerscough and Whitehead, 1967; Rorison, 1968; Higgs and James, 1969; Foulds, 1970) and the results of supplementary experiments confirm that the measurements adequately distinguish between species of inherently slow and inherently rapid maximum relative growth rate, $RGR_{(max)}$, where $RGR_{(max)}$ is derived from the slope of the linear regression of $\log_e$ (plant dry weight) against time for four harvests over the period 2–5 weeks after germination.

The values of $RGR_{(max)}$ each refer to a seed sample from one field population. In view of the possibility of intraspecific variation in $RGR_{(max)}$,

inferences from these estimations have been restricted to those based upon comparisons between groups of species (see Figures 3 and 7).

(iii) *Greenhouse experiments.* Using a standardized mixture of seeds of native species, grassland vegetation has been synthesized in large containers and attempts have been made to study the role of competition in the regulation of species density.

The results of the investigation confirm that several factors are involved in the control of species density. This paper is concerned with two of these: (a) stress imposed by the environment or by management, and (b) competition. An attempt is made to describe the involvement of these two factors in the control of species density and to suggest criteria by which their impact at individual sites or in different types of vegetation may be assessed.

2. Low species densities associated with conditions of stress

In Figure 1, habitats sampled extensively over the same geographical area are compared with respect to mean and range in species density. It is clear that values rarely exceed 40 species/m^2 and that, in the majority of habitats, species density varies widely. In a number of habitats, however, a high proportion of the samples exhibit low species density. When these habitats are examined it is apparent that they include several specialized environments in which low species densities arise from the small number of species in the local flora (or possibly in the British flora) adapted to withstand the extreme conditions, whether environmentally determined (e.g. heavily contaminated lead mine spoil) or arising from management (e.g. severely trampled ground) or through the combined effect of the two (e.g. shaded paths).

A characteristic of these habitats is the presence of species of narrow ecological range, many of which are therophytes. Examples of species characteristic of situations where low species density coincides with particular conditions of extreme stress are cited in Table 1.

TABLE 1. Selected examples of species characteristic of vegetation of low species density in extreme habitats

Habitat	Species
Highly acidic pasture	*Deschampsia flexuosa, Nardus stricta*
Shallow limestone outcrops	*Sedum acre, Erophila verna*
Lead mine spoil	*Minuartia verna, Thlaspi alpestre*
Paths	*Poa annua, Plantago major*

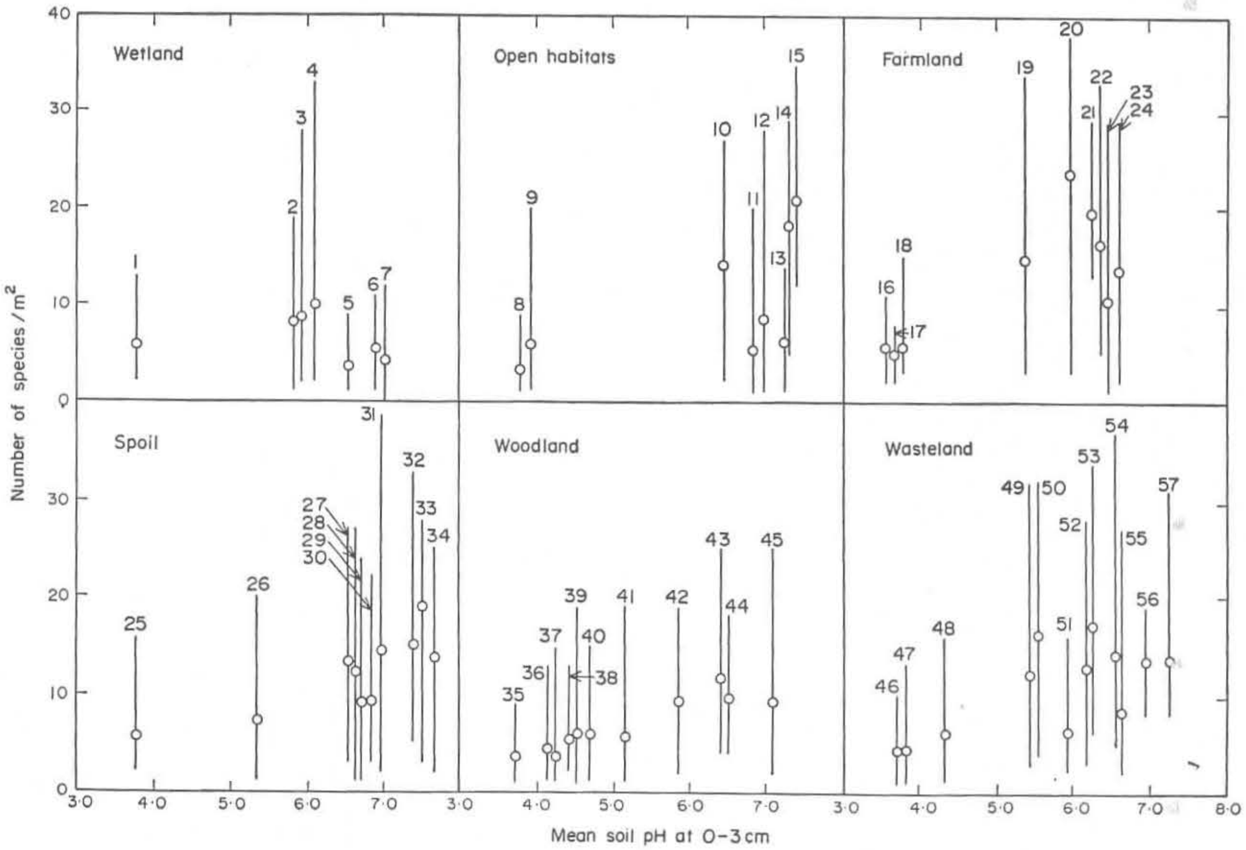
Wetland
Open habitats
Farmland
Spoil
Woodland
Wasteland
Number of species / m²
Mean soil pH at 0–3 cm

Figure 1. Mean and range in species density in the one square metre samples of vegetation examined in the major habitats present in an area of 900 square miles around Sheffield, Yorkshire. Bare ground was not sampled; hence the minimum value possible is one.

Key to habitats. 1, unshaded mire on non-calcareous strata, soil pH < 4·1; 2, shaded mire; 3, unshaded mire on calcareous strata; 4, unshaded mire on non-calcareous strata, soil pH > 4·0; 5, lakes, ponds, canals, ditches, depth of water < 11 cm; 6, lakes, ponds, canals, ditches, depth of water > 10 cm; 7, rivers and streams; 8, non-calcareous cliffs; 9, rock outcrops on non-calcareous strata; 10, consolidated limestone scree; 11, walls; 12, limestone cliffs; 13, unconsolidated limestone scree; 14, rock outcrops on Magnesian Limestone; 15, rock outcrops on Carboniferous Limestone; 16, unenclosed pasture on Millstone Grit; 17, unenclosed pasture on limestone, soil pH < 4·1; 18, unenclosed pasture on Coal Measures; 19, enclosed pasture; 20, unenclosed pasture on limestone, soil pH > 4·0; 21, permanent meadows; 22, fallow arable; 23, arable, crop broad-leaved; 24, cereal arable; 25, coal mine heap, soil pH < 4·1; 26, coal mine heap, soil pH > 4·0; 27, lead mine waste, discontinuous vegetation cover; 28, cinders; 29, manure and sewage residues; 30, lead mine waste, continuous vegetation cover; 31, heaps of mineral soil (building sites etc.); 32, spoil heaps in limestone quarries (Carboniferous Limestone); 33, spoil heaps in limestone quarries (Magnesian Limestone); 34, brick and mortar rubble; 35, plantations of broad-leaved trees, soil pH < 4·1; 36, woodland on Bunter Sandstone; 37, coniferous plantations; 38, scrub on non-calcareous strata; 39, woodland on Millstone Grit; 40, woodland on Coal Measures; 41, plantation of broad-leaved trees, soil pH < 4·1; 42, woodland on Magnesian Limestone; 43, scrub on limestone; 44, hedgerows; 45, woodland on Carboniferous Limestone; 46, derelict grassland and heath on Bunter Sandstone, soil pH < 4·1; 47, derelict grassland and heath on Millstone Grit; 48, derelict grassland and heath on Coal Measures; 49, derelict grassland and heath on Bunter Sandstone, soil pH > 4·0; 50, derelict grassland and heath on Carboniferous Limestone; 51, shaded paths; 52, river banks etc.; 53, woodland on Magnesian Limestone; 54, unshaded paths with incomplete vegetation cover; 55, unshaded paths with complete vegetation cover; 56, road verges, mown frequently; 57, road verges, mown annually or unmown.

Of the habitats in which species density is reduced by environmental stress, the most extensive are those which occur on highly acidic soils. From Figure 1 it is apparent that, regardless of the vegetation type, species densities are consistently low where the surface soil pH is less than 4·1. More specific evidence of limitation of species density by the small number of species adapted to strongly acidic soils is presented in Figure 2, which is based upon 593 randomly located one square metre quadrats from 43 areas of unmanaged grassland widely distributed throughout the survey area. Maximum species density is roughly constant over the range pH 4·0–8·0 but on more acidic soils there is an abrupt decline despite a four-fold increase in the number of samples examined. Over the pH range 6·0–3·0 the total number of species recorded falls continuously from 157 to 38. When the species which occurred rarely and with low abundance are discounted, it is found that, in the samples corresponding to the soil pH range 3·0–3·5, the maximum number of species recorded in a single one square metre quadrat (nine) approaches the total number of species recorded from 129 quadrats (fourteen).

From Figure 2 it is clear that the close correlation between mean species density and the total number of species recorded in each pH category

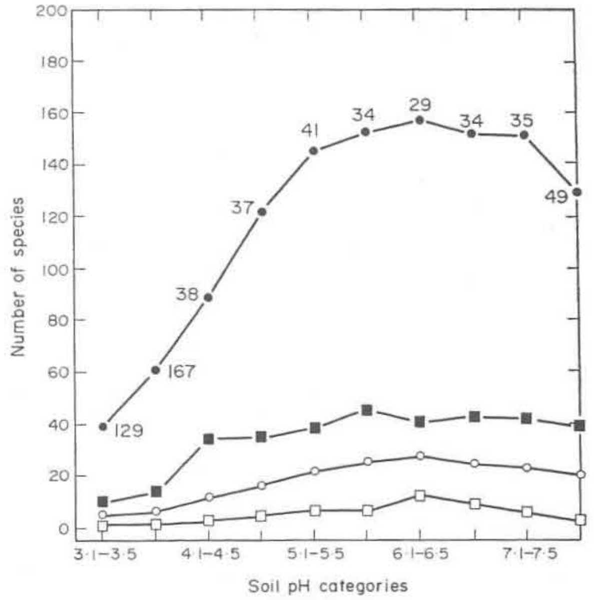

Figure 2. Mean (○), maximum (■), and minimum (□) species density and total number of species represented (●) in categories of surface soil pH encountered in 593 one square metre quadrats located at random in unmanaged grassland. The values inserted on the topmost curve refer to the number of quadrats falling in each half-unit soil pH category.

extends over the full range in soil acidity (pH 3·0–8·0). This suggests that the two may be causally related even on non-acidic soils and that, where samples are to be compared in an attempt to recognize the relationship of other factors to species density, whenever possible comparison should be restricted to samples with a similar range in soil pH.

Factors other than the small number of adapted species may contribute to the reduction of species density in the vegetation on highly acidic soils. However, the importance of this mechanism is supported by experimental evidence (Grime and Hodgson, 1969; Hodgson, 1972) which suggests that only a relatively small number of native species are adapted nutritionally to exploit highly acidic soils.

3. Low species densities associated with competitive exclusion

Although the importance of competition in natural interactions between plant species is established beyond dispute, there are no simple generally-accepted criteria by which to recognize field situations in which competition is the primary factor limiting species density. The recent application of the concept of dominance to studies of species density (Whittaker, 1965; McNaughton, 1968) is not helpful in this respect. " Dominants " have usually been recognized as species which account for a high proportion of the annual production of standing crop. This criterion fails to distinguish between situations in which competitive exclusion is occurring and those in which the predominant species owe their success to tolerance of conditions in which species density is reduced by the direct effects of stress imposed by environment or management.

An alternative approach attempted here is to identify the biological characteristics which confer the ability to exclude other species by competition, and to classify herbaceous plants according to the extent to which these characteristics are evident in the genotype. Vegetation in which low species densities arise from competitive effects may then be recognized by the presence at high frequency of species objectively classified as those capable of competitive exclusion.

In order to attempt to identify the characteristics of species of high competitive ability reference has been made to published investigations of inter-specific competitions in field or laboratory (Olsen, 1921; Greig-Smith, 1948; Monsi and Saeki, 1953; Watt, 1955; Black, 1958; Donald, 1958; Thurston, 1969; Black, 1960; Palmer and Sagar, 1963; Ellenberg, 1963; Willis, 1963; Grime, 1963; Smith, Elston and Bunting, 1971; Maarel, 1971). Four consistent features of " competitive " species are (a) tall stature, (b) a growth form (usually a large densely-branched rhizome or expanded tussock

structure) which allows extensive and intensive exploitation of the environment above and below ground, (c) a high value of $RGR_{(max)}$, (d) a tendency to deposit a dense layer of litter on the ground surface. It has proved practicable to score plant species with respect to each of these features and to use the sum of the scores to provide a competitive index over a scale of 0–10 (Table 2).

TABLE 2. Examples illustrating the derivation of the competitive index†

Species	Attributes (a)	(b)	(c)	(d)	Competitive index (Total/2)
Chamaenerion angustifolium	5	5	5	2	8·5
Arrhenatherum elatius	5	4	4	3	8·0
Brachypodium pinnatum	3	4	3	5	7·5
Ranunculus repens	3	5	3	1	6·0
Helictotrichon pratense	3	2	3	2	5·0
Taraxacum officinale	3	1	4	1	4·5
Festuca ovina	2	1	3	2	4·0
Campanula rotundifolia	2	2	3	0	3·5
Arenaria serpyllifolia	1	0	4	0	2·5

† *Key to scoring system.* (a) Maximum plant height (Clapham, Tutin and Warburg, 1962). 1, <26 cm; 2, 26–50 cm; 3, 51–75 cm; 4, 76–100 cm; 5, >100 cm. (b) Morphology (Clapham, Tutin and Warburg, 1962; personal observations during surveys). 0, Small therophytes; 1, robust therophytes; 2, perennials with compact unbranched rhizome or forming small (<10 cm diameter) tussock; 3, perennials with rhizomatous system or tussock, attaining diameter 10–25 cm; 4, perennials attaining diameter 26–100 cm; 5 perennials attaining diameter > 100 cm. (c) Relative growth rate (Grime and Hunt, in preparation). 1, $RGR_{(max)} < 2{\cdot}1$ mg g^{-1} h^{-1}; 2, 2·1–4·0 mg g^{-1} h^{-1}; 3, 4·1–6·0 mg g^{-1} h^{-1}; 4, 6·1–8·0 mg g^{-1} hg^{-1}; 5, >8·0 m g^{-1} h^{-1}. Where no estimate is available a provisional score of 3 has been used. (d) Maximum accumulation of persistent (i.e. from one growing season to the next) litter produced by the species (personal observations during surveys). 0, None; 1, thin, discontinuous cover; 2, thin, continuous cover; 3, up to 1 cm depth; 4, up to 5 cm depth; 5, >5 cm depth.

As it has been calculated in this paper, the competitive index incorporates a subjective component, fails to take account of ecotypic variation and ignores certain competitive attributes such as the release of phytotoxic compounds. However, despite this lack of refinement the index appears to have considerable predictive value. Data such as those illustrated in Figure 3 (see also Grime, 1973) confirm that where species of high competitive index are prominent, species densities are consistently low.

A possible objection to the competitive index is that it is based upon attributes found to be advantageous in competitions in productive habitats. It may be argued that different characteristics confer competitive ability in unproductive habitats. It would appear, however, that although competition

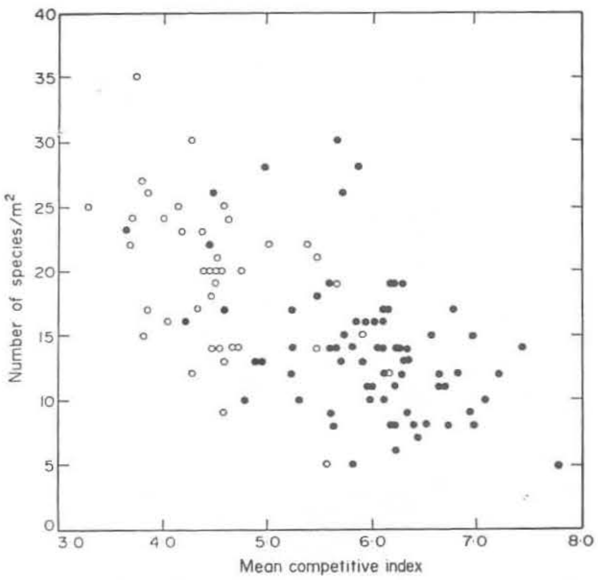

Figure 3. The relationship between " site competitive index " and species density in two habitats of contrasted productivity, sampled widely from the same geographical area. (●, Roadside verges; ○, limestone outcrops with discontinuous cover of soil and vegetation.) " Mean competitive index " is a mean value derived from the competitive indices of all species present in the sample, each weighted according to its frequency within the quadrat.

(especially that for water and nutrients) is not restricted to productive habitats, its importance in unproductive habitats is small relative to the direct impact of environmental stress. It is suggested moreover that differences in competitive ability (as measured by the competitive index) reflect a fundamental dichotomy in the adaptive strategy of herbaceous plants and are the result of the conflicting selection pressures exerted, in productive habitats, by competition and, in unproductive habitats, by environmental stress. From a wide range of comparative studies (Ashton, 1958; Pigott and Taylor, 1964; Grime and Jeffrey, 1965; Grime, 1965; Grime, 1966; Clarkson, 1967; Myerscough and Whitehead, 1967; Hutchinson, 1967; Loach, 1967; Rorison, 1968; Parsons, 1968*a*, *b*; Higgs and James, 1969; Hunt, 1970; Foulds, 1970; Loach, 1970) there is accumulating evidence that characteristics such as tall stature, rapid potential growth-rate (and, incidentally, high phenotypic plasticity with respect to the deployment of photosynthate, e.g. increase in leaf area in shade and increase in root: shoot ratio under mineral nutritional stress), all of which tend to maximize dry matter production under productive and competitive conditions, are of low selection value in circumstances of extreme environmental stress.

4. High species densities

Calculation of the mean competitive indices of samples from the various circumstances in which high species densities are recorded reveals that species of high competitive ability are scarce or occur with reduced frequency (Figure 3 and see also Grime, 1973). On the basis of previous studies (e.g. Thurston, 1969; Willis, 1963; Pigott and Taylor, 1964; Grime, 1966; Clarkson, 1967; Hutchinson, 1967; Loach, 1967; Parsons, 1968*a*, *b*; Newhouse and Madgwick, 1968; Higgs and James, 1969; Loach, 1970; Maarel, 1971) and the results of this investigation, it is suggested that two mechanisms cause the suppression of species of high competitive index in species-rich vegetation. One mechanism coincides with low productivity and is the result of environmental stress induced by factors such as drought and mineral nutrient deficiencies and the other is brought about by forms of management such as grazing, mowing, burning and trampling, which tend to prevent potentially competitive species from attaining maximum size and vigour.†

Experimental evidence suggests that species of high competitive index are particularly susceptible to changes in productivity and that alteration in the vigour of these plants is associated with an inverse effect on species density. The addition of mineral fertilizers to nutrient-deficient vegetation has been found to cause an expansion in species of high competitive index, with a marked reduction in species density (Thurston, 1969; Willis, 1969; Jeffrey, 1971). Conversely, treatment of productive vegetation with the growth retardant maleic hydrazide tends to suppress species of high competitive index and to increase species density (Yemm and Willis, 1962).

The Sheffield surveys provide circumstantial evidence of the importance of management in the maintenance of high species densities in certain habitats. From Figure 1 it is clear that managed vegetation (e.g. pastures and meadows), in general, display species densities higher than those in unmanaged habitats. The impact of management is most apparent when species densities in derelict sheep pastures of the Derbyshire dales are compared with those from neighbouring dales in which sheep grazing has been maintained to the present day. From comparisons such as that illustrated in Figure 4 there is evidence that the beneficial effect of continued grazing upon species density extends over the full spectrum of grasslands associated with the soil pH range 4·0–8·0.

A close parallel may be drawn therefore between the influence of increasing environmental stress and of increasing intensity of management upon species density. According to the model proposed in Figure 5(a), under conditions

† Henceforward " management " is applied in this restricted sense.

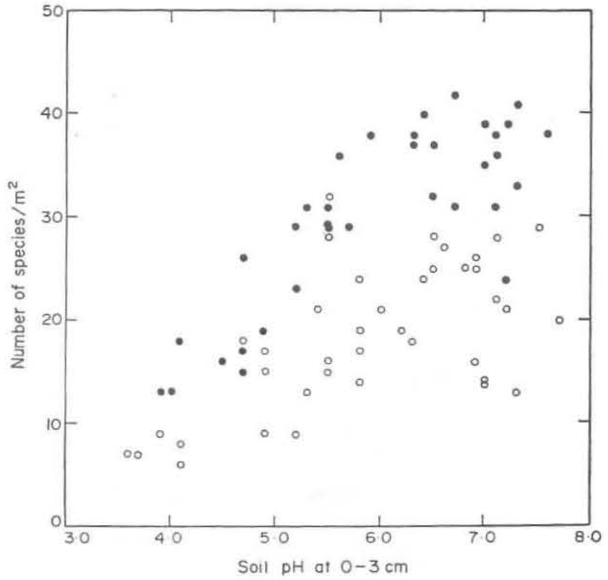

Figure 4. Comparison of species densities in unenclosed grassland in two Derbyshire dales differing in management. (●, Cressbrookdale; grazing by sheep and cattle. ○, Lathkilldale, ungrazed, burned sporadically.) The samples refer to one square metre quadrats located at random.

of low environmental stress, productivity is high and species of high competitive index attain maximum vigour and species density is low due to competitive exclusion. Under conditions of increased environmental stress, the competitive species decline in vigour and species of lower competitive ability are able to survive. With further reductions in productivity, species density falls as conditions of extreme environmental stress are reached and species density is limited by the scarcity of species tolerant of the specific conditions limiting productivity. This model is consistent with the observation of Odum (1963) that " the greatest diversity occurs in the moderate or middle range of a physical gradient ". Data conforming to the model have been obtained from transects along naturally-occurring gradients in environmental stress (Grime, 1973).

With respect to the gradient of increasing intensity of management (Figure 5(b)) the pattern is essentially similar. Assuming that productivity is sufficiently high, competitive exclusion will occur at low intensity of management. With more intensive management, species of high competitive index are suppressed and conditions favourable to less aggressive species obtain. At the highest rates of management, species density would be expected to fall as a situation is reached in which only a small number of species are tolerant

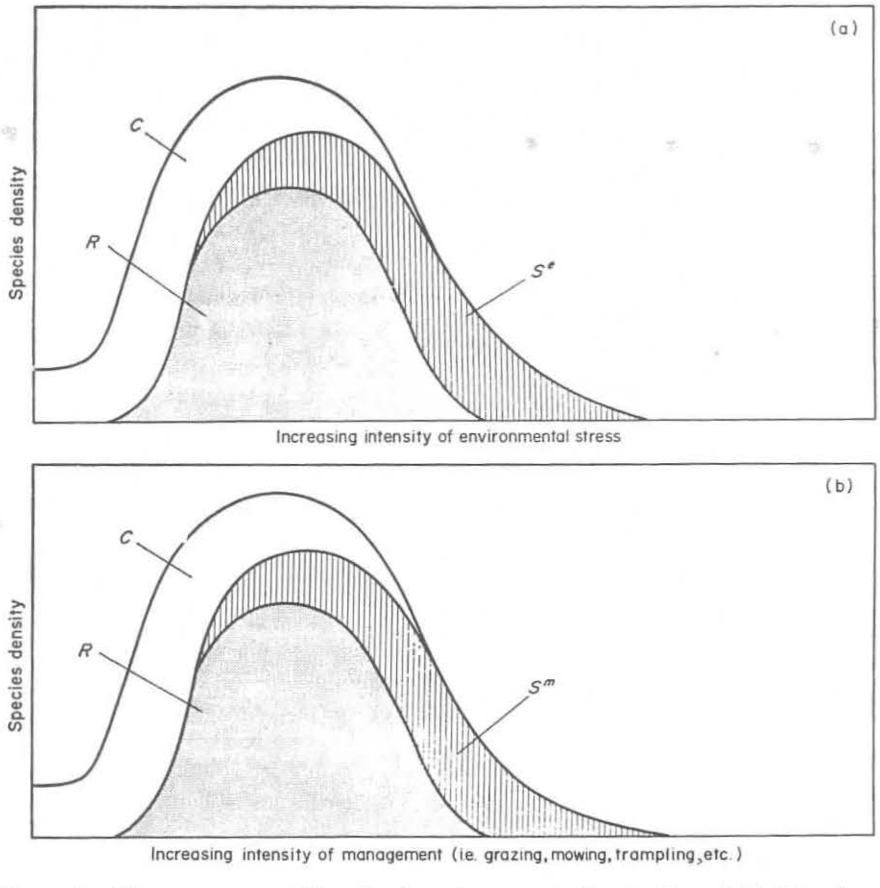

Figure 5. Diagrams representing the impact upon species density of (a) intensity of environmental stress and (b) intensity of management. *C*, Species of high competitive index. S^e, S^m, Species (or ecotypes) of high resistance to the prevailing stresses imposed by environment or by management respectively. *R*, Remaining species.

of the specific impact of the management applied. It is difficult to find situations in the field which illustrate all features of the latter model. Gradients in intensity of management rarely extend over the full range represented in Figure 5(b). A possible exception to this arises in conditions of excessive trampling (Grime, 1973) although here the possibility must be recognized that a significant component of the trampling effect is due to factors such as soil compaction and is more correctly attributable to environmental stress.

The two mechanisms illustrated in Figure 5 only rarely operate in isolation from each other. In the majority of species-rich habitats the mechanism by

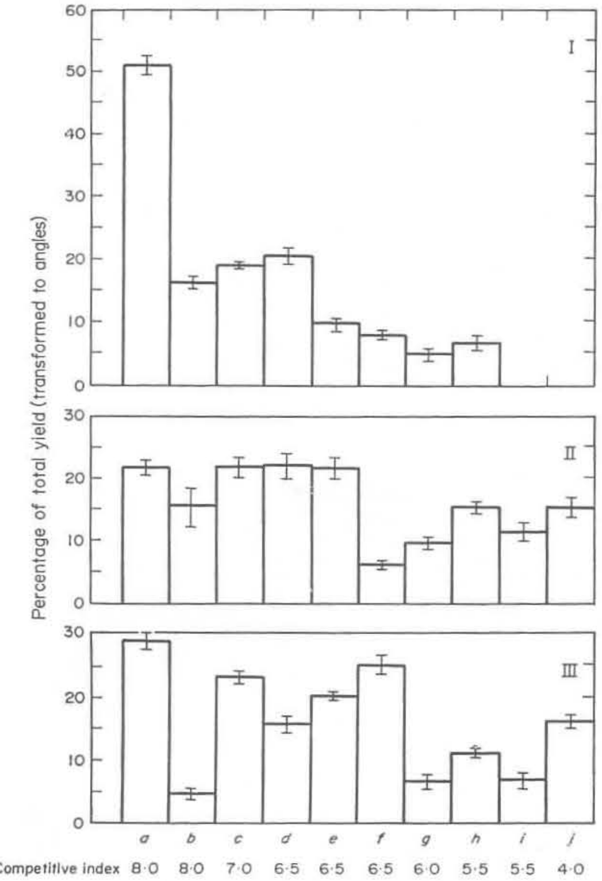

Figure 6. Histograms comparing the effect of nitrogen deficiency and frequent mowing upon the species composition of turf synthesized from a standardized seed mixture. The experiment was carried out in a greenhouse in 36-l containers of sand watered with Hewitt nutrient solution. Seedling counts showed no effect of treatment upon initial establishment. The experiment was harvested after seven months. I. Control, nitrogen 170 parts/10^6, unmown. II. Nitrogen 5 parts/10^6, unmown. III. Nitrogen 170 parts/10^6, mown weekly at 6 cm. Yield and confidence limits are presented as percentage of standing crop transformed to angles.
Key to species. (a) *Arrhenatherum elatius*, (b) *Agropyron repens*, (c) *Dactylis glomerata*, (d) *Holcus lanatus*, (e) *Lolium perenne*, (f) *Agrostis tenuis*, (g) *Festuca rubra*, (h) *Bromus erectus*, (i) *Anthoxanthum odoratum*, (j) *Festuca ovina* (Mahmoud and Grime, unpublished).

which highly competitive species are suppressed is the result of an unknown combination of the two factors. The parallel influence of environmental stress and of management upon the status of species of high competitive index is illustrated in Figure 6, which describes the result of an experiment in which environmental stress (represented by nitrogen deficiency) and management (represented by frequent cutting) were applied to grassland synthesized

from a standardized seed mixture of native species. The data confirm that species of high competitive index may be suppressed by both low productivity associated with environmental stress and by intensive management, and illustrate the difficulty which may be encountered in distinguishing the effects due to the two mechanisms.

From a practical standpoint, therefore, there is a need to determine the relative importance of environmental stress and management in maintaining high species density at particular sites. The minimum requirement in order to achieve this is a measurement, either of net environmental stress or of the intensity of management. Both of these are difficult to measure directly and rapidly, mainly because of the need to integrate the effects of different forms of stress or management respectively. A possible solution to this problem is to recognize the inverse relationship between net environmental stress and productivity, and to use the potential growth-rates of the perennial species present at each site to derive an index of the latter. A correlation between potential growth-rates and site productivity may be inferred from a number

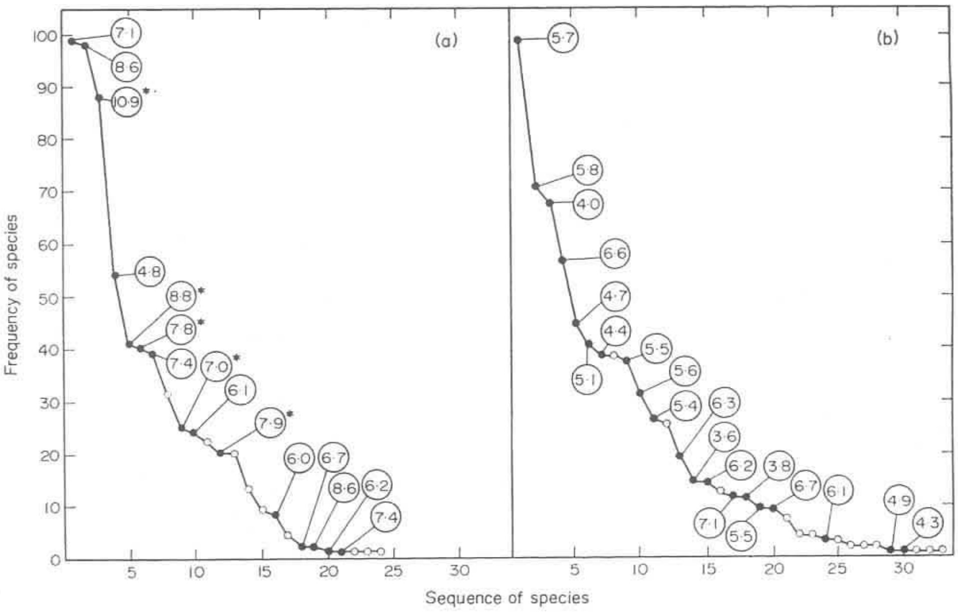

Figure 7. Comparison of 2 one square metre samples of species-rich vegetation with respect to the potential growth-rates of the component species. (a) Productive meadow (Coombsdale, Derbyshire); (b) ancient limestone pasture (Cressbrookdale, Derbyshire). In each figure the species are arranged in order of decreasing % occurrence in 10×10 cm subdivisions of the one square metre quadrat. The encircled values refer to the $RGR_{(max)}$ of the species. The open circles indicate species for which no growth-rate estimations are available. * Species of high (> 6·0) competitive index.

of studies (de Boer and Ferrari, 1957; Kruijne, 1960; Bradshaw *et al.*, 1964; Grime, 1966). The screening of plant growth-rates reported in this paper provides further evidence of this relationship. Comparisons such as that illustrated in Figure 7 reveal a consistent difference between productive and unproductive vegetation with respect to the potential growth-rates of the component species.

A productivity index based upon values of $RGR_{(max)}$ for the component perennial species would appear to be valuable, not only in field assessments of the intensity of management necessary to initiate or maintain high species density, but also as a guide to the stability of the vegetation under study. It is to be expected that vegetation composed of species with high potential growth-rates (especially where some are suppressed specimens of species of high competitive index, Figure 7(a)) will show a rapid decline in species density when management is relaxed. Where values for $RGR_{(max)}$ are low any reduction in species density is likely to proceed at a relatively slow rate.

5. Additional factors

In this paper, differences in species density have been related to two factors: variation in stress imposed by environment or by management, and variation in the frequency and vigour of species of high competitive ability. In the maintenance of low species densities both factors appear to exercise a direct controlling effect. With respect to the control of high species densities, additional mechanisms are involved. The absence of extreme stress and the suppression of species capable of competitive exclusion are preconditions for high species density. Realization of a high species density depends upon the accessibility of the site to suitable species and, in some situations at least, upon the existence of conditions which allow species of different biology to survive in close proximity to each other. This latter phenomenon appears to have a number of possible causes including small-scale heterogeneity in environment, selective effects of management and temporal variation in environment and management. Additional criteria which allow field assessments of the impact of site accessibility and degree of niche-differentiation upon species density will be reported elsewhere.

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